On the Development of the Hypobranchial, Branchial, and Laryngeal Muscles of Ceratodus. With a Note on the Development of the Quadrate and Epihyal.

By

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With 39 Text-figures.

As is well known, Wiedersheim stated that laryngeal muscles exist in Lepidosiren and Protopterus, but are absent in Ceratodus. He admitted, however, that the specimen investigated was badly preserved.

In a recently published paper (1920) on the laryngeal muscles of Amphibia, I suggested that, possibly, they might be found in better specimens. Owing to the skill and perseverance of Dr. Bancroft I have come into possession of some well-preserved heads, and also of a series of embryos up to the stage of 30 mm. in length for purposes of investigation. The material also enabled me to examine the development of the hypobranchial and pharyngeal muscles, which, together with other structures, have been the subject of an elaborate memoir by Greil. In the description given by Semon of the development of Ceratodus the embryos were depicted in a series of stages numbered from 1 to 48, the last mentioned and oldest stage described being an embryo of 17·8 mm. Greil's description is based on Semon's stages, and also extended to stage 48. The embryos described in this paper had been fixed in formalin, and their lengths are given in millimetres. Their relation to Semon's stages will be found in an appendix.

A tabular statement of the synonyms of the names employed has also been appended.

Occipital Myotomes and Nerves. Fürbringer (1897) stated that, in the adult stage of Ceratodus, there are two or three occipital and two occipito-spinal nerves.

x_v	y_{vd}	z_{vd}	a_{vd}	b_{vd}		
	y_v	z_{vd}	a_{vd}	b_{vd}		
	y_v	z_v	a_{vd}	b_{vd}		
	y_v	z_v	a_{vd}	b_{vd}	c_{vd}	c coming out between skull and vertebra.

The Plexus cervicalis is formed from x, y, z, or y, z. Sewertzoff (1902) stated that in a 15·7 mm. embryo there are five occipital myotomes in front of the first vertebral arch, the first two being in process of reduction. There are ventral spinal roots corresponding to the fourth and fifth. He identified the fourth myotome with x of Fürbringer, so that the first five are u, v, w, x, y.

Greil (1918) stated that no vertebral arches are present in a 15·7 mm. embryo, and that they are developed in a 17·8 mm. embryo. Five occipital myotomes are present in front of the first vertebral arch in the latter stage. The first two have no corresponding nerve-roots, the third has a (variable) ventral root, the fourth a ventral root, and the fifth a ventral and a (variable) dorsal root. The Nervus hypobranchialis (which = the Plexus cervicalis of Fürbringer) is formed from the variable third, and the fourth and fifth nerve-roots. He identified these five myotomes with v, w, x, y, z of Fürbringer's terminology.

On comparison of these statements it would appear that (1) Sewertzoff's 15·7 mm. embryo was a little more advanced in development than Greil's 17·8 mm. embryo—vide infra. The embryos I have examined at these stages agree with those of Greil, so that, in all probability, Sewertzoff's embryo was somewhat shrunken. (2) Sewertzoff regarded the fourth myotome—counting from before backward—and Greil the third myotome as myotome x of Fürbringer's classification. The explanation of the difference of opinion is that Sewertzoff's embryo was one in which the variable nerve x was absent. The variation certainly occurs, e.g. in an embryo of 20 mm. Nerves x, y, z were present; in one of 26 mm. (vide Text-fig. 26) there were only nerves y and z. I therefore follow Greil's nomenclature. Atrophy of myotomes takes place from before backwards, as stated by Sewertzoff. Thus in a 20 mm. embryo only a few fibres of myotome v persisted, in one of 24 mm. myotome v has altogether disappeared and also the ventral part of myotome w.

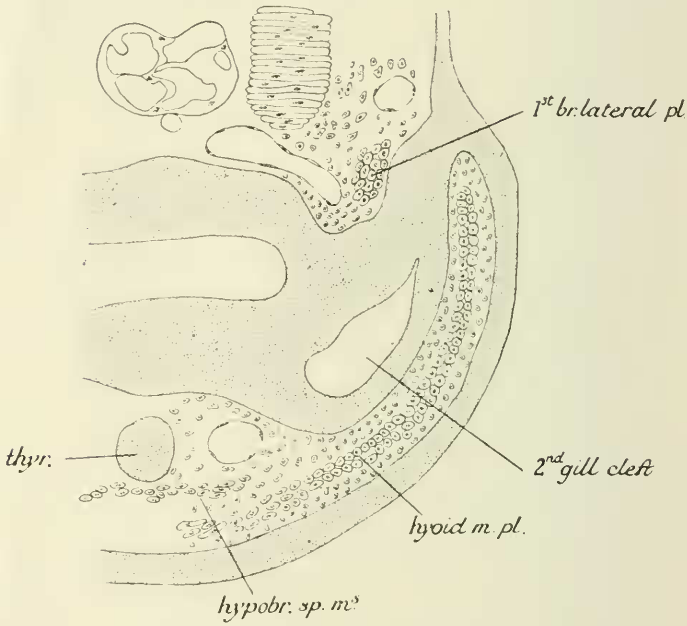
Coraco-hyoideus and Genio-coracoideus. Greil stated that the Coraco-hyoideus is developed from downgrowths of the third to the sixth myotomes, i.e. myotomes x, y, z, a. These downgrowths separate from the myotomes above, fuse together, and form the Coraco-hyoideus, which extends from the shoulder-girdle to the hyoid bar. The primordium of the Genio-coracoideus separates from the ventral edge of the third myotome (i. e. foremost) constituent of the Coraco-hyoideus in a 13·9 mm. embryo, and fuses with its fellow, forming a median muscle which elongates forwards to the jaw and backwards. The posterior end forks right and left, and in a 17·8 mm. embryo—the latest stage investigated—reaches the antero-posterior level of the first branchial arch. This method of development of the anterior constituent of the hypobranchial spinal muscles is not a usual one, and the initial stages were not depicted. The first figures given, i. e. Nos. 424–9, show the Genio-coracoideus already developed as a median muscle, partly in front of and partly underlying the anterior ends of the Coraco-hyoidei.

I find that in a 9·5 mm. embryo (Text-figs. 1–5) the pericardium extends forwards to the hyoid segment, and its anterior end is ventral to the hinder edge of the thyroid outgrowth. The primordium of the hypobranchial spinal muscles lies laterally to the pericardium, and, as this lessens in size, approximates to its fellow. In front of the pericardium the two columns come together and lie beneath the thyroid. The anterior part of the primordium consists solely of yolk-laden cells, the posterior part of muscle-cells.

In a 10·5 mm. embryo (Text-figs. 6–9) the pericardium has

TEXT-FIGS. 1–5.

Embryo 9·5 mm., transverse sections; Text-fig. 1 is the most anterior.

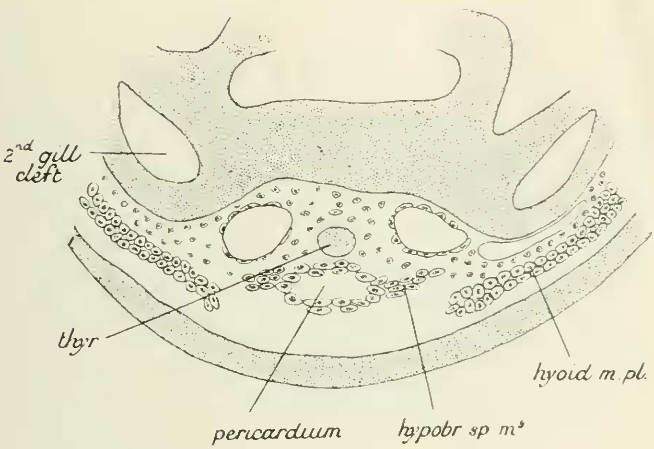


ABBREVIATIONS TO TEXT-FIGURES.

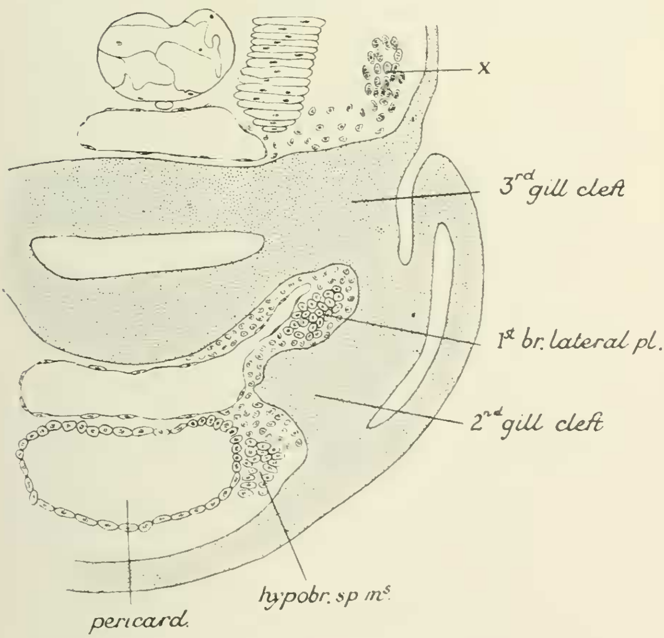
aud. cap., auditory capsule. *ceratobr.*, ceratobranchial. *coraco-hy.*, Coraco-hyoideus. *const. br.*, Constrictor branchialis. *epi-br.*, epibranchial. *genio-cor.*, Genio-coracoideus. *g. petros.* ix, ganglion petrosum ix. *hypobr. sp. ms.*, primordium of hypobranchial spinal muscles. *lateral pl.*, lateral plate. *lev.*, Levator arcus branchialis. *m. pl.*, muscle-plate. *Mx.*, myotome x. *Nx.*, nerve x. *operc.*, opercular fold. *parachord. c.*, parachordal cartilage. *pericard.*, pericardium. *peric. perit. duct*, pericardio-peritoneal duct. *thyr.*, thyroid body. *1st vert. arch*, 1st vertebral arch. Roman numerals, cranial nerves.

retreated a little, and its anterior end is 56 μ behind the thyroid. The primordium of the hypobranchial muscles has separated into anterior and posterior parts—the Genio-coracoideus and

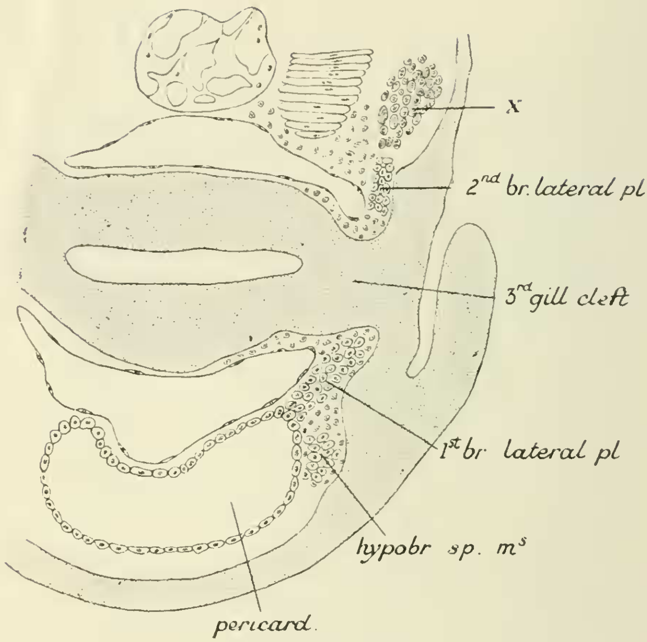
TEXT-FIG. 2.



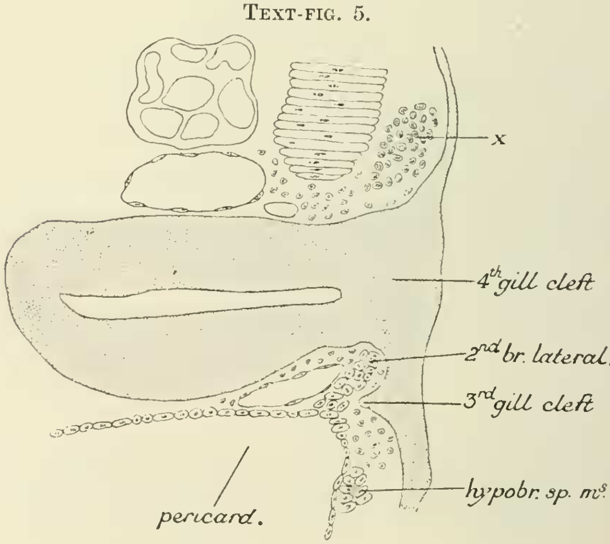
TEXT-FIG. 3.



TEXT-FIG. 4.



TEXT-FIG. 5.



the Coraco-hyoideus. The Coraco-hyoideus lies laterally to the pericardium, and its anterior end is 56 μ behind the thyroid. The Genio-coracoidei form a λ-shaped structure. The anterior median part is ventral to the thyroid: it extends behind this for 104 μ, diverging into two lateral ends which lie beneath the anterior ends of the Coraco-hyoidei. The Genio-coracoidei consist of yolk-laden cells, the Coraco-hyoidei of muscle-cells. In an 11 mm. embryo the anterior end of the Genio-coracoidei extends a little farther forwards—in front of the thyroid, and in a 12 mm. embryo reaches Meckel's cartilages. Its cells become transformed into muscle-cells in a 13 mm. embryo.

The Genio-coracoidei extend slowly backward, diverging into right and left halves. These reach the level of the third branchial arch in a 20 mm. embryo, and become attached to the lateral edges of the median cartilage—called 'sternum' by Greil—which forms the ventral constituent of the cartilaginous shoulder-girdle, in the 28 mm. embryo.

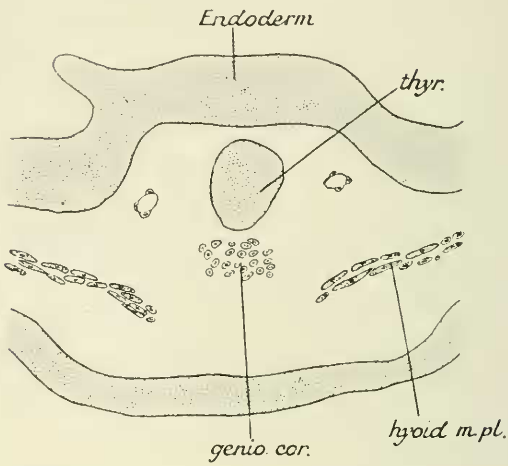
The above may be summarized in the statement that the primordium of the hypobranchial spinal muscles extends forwards, laterally to the pericardium, and in front of this joins its fellow. It then separates into Genio-coracoideus and Coraco-hyoideus. The Genio-coracoidei, in contact with each other from the first, form a median structure which extends forwards to the jaw and backwards to the shoulder-girdle.

Fürbringer stated that the Genio-coracoideus of the adult form extends from the mandible to the shoulder-girdle (coracoid and clavicula) and has one tendinous inscription on its inner, i. e. dorsal surface. This, he said, gives rise to the idea that it originally consisted of two myomeres, but this structure may be secondary. This latter supposition is confirmed by the fact that in a 28 mm. embryo (in which the posterior end of the muscle has reached the 'sternum') there are no inscriptions in the muscle. The same explanation applies to the three inscriptions depicted in the muscle by Maurer.

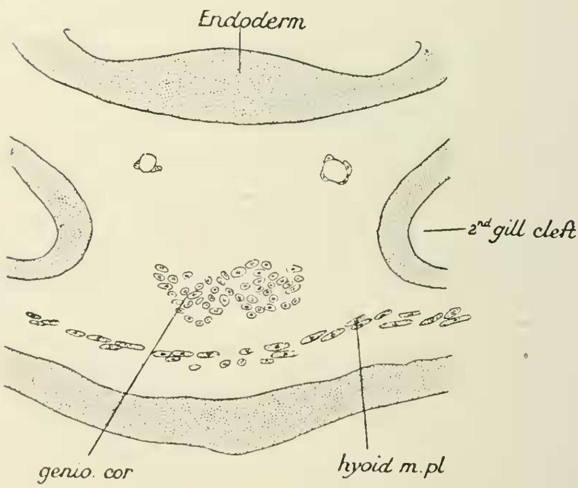
Innervation.—Fürbringer stated that the Coraco-hyoideus and Genio-coracoideus are innervated by the Plexus cervicalis, i. e. Nervi spinales x, y, z, or y, z.

TEXT-FIGS. 6–9.

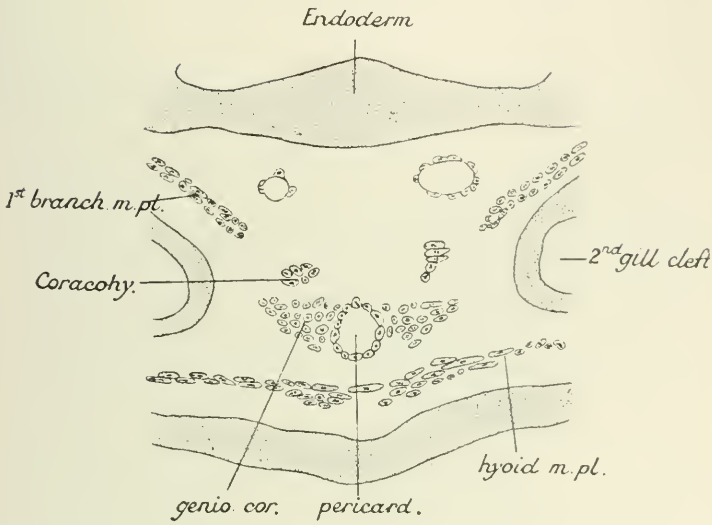
Embryo 10·5 mm., transverse sections; Text-fig. 6 is the most anterior.



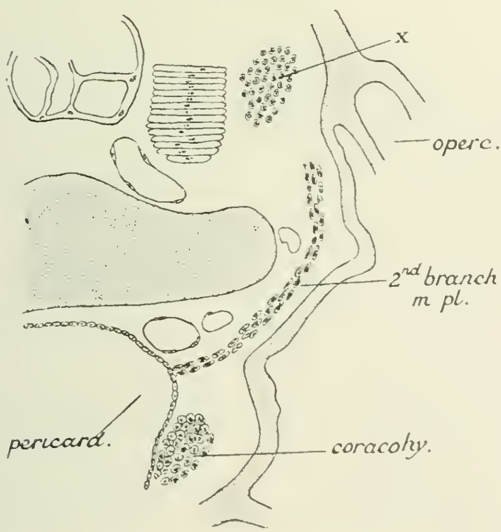
TEXT-FIG. 7.



TEXT-FIG. 8.



TEXT-FIG. 9.



Greil stated that the Coraco-hyoideus is innervated by the N. hypobranchialis (derived from Ni. occips. x, y, z, or y, z) and by the R. hypobranchialis of N. occipito-spin. a, whilst the Genio-coracoideus is innervated by the R. hypohyoideus of N. posttrematicus ix. He did not refer to Fürbringer's statement.

I find in a 27 mm. embryo that an anterior branch of the N. hypobranchialis enters the posterior end of the Genio-coracoideus, and have not found any branch of the IXth nerve entering the muscle.

The Genio-coracoideus and Coraco-hyoideus of Ceratodus are homologous with the Genio-thoracicus and Coraco-hyoideus of Protopterus and Lepidosiren. Agar has shown that the latter is developed from myotomes x, y, z ; but did not describe the development of the Genio-thoracicus.

The Genio-coracoideus of Ceratodus resembles the Genio-coracoideus s. Coraco-mandibularis of Selachii and the Genio-branchialis s. Branchio-mandibularis of Ganoids in that it is formed from the anterior constituent of the hypobranchial spinal muscles and subsequently grows backwards overlapping the posterior constituent—Coraco-hyoideus.

On the Source of the Branchial Muscles.—Greil stated that in a 5·9 mm. embryo the mesoderm lateral to the branchial region of the alimentary canal—between this and the ectoderm—is continuous with the epithelium of the pericardium, and is to be regarded as ' lateral-plate '. In 6·6 to 9·8 mm. embryos these lateral plates degenerate into connective tissue, and their place is taken by downgrowths from the first and second myotomes. The cells of these downgrowths are distinguishable from those of the lateral plates by the shape of their nuclei and the later absorption of their yolk-granules. Processes from the first myotomes penetrate the first three branchial arches, whilst one from the second myotome forks over the sixth gill-cleft into the fourth and fifth arches. In a 10·2 mm. embryo these downgrowths separate from the myotomes above and become the source of the branchial musculature.

I find that in an embryo of 9·5 mm. (Text-figs. 1–5) the cell-columns in the first and second branchial segments, which consist of yolk-laden cells, are not continuous with the myotome above, but are continuous with the pericardial wall below. I interpret them as lateral plates. In an embryo of 10·5 mm. (Text-figs. 6–9) the pericardium has retreated a little, and its anterior end is 56 μ behind the thyroid, just in front of the lower end of the first branchial segment. In this segment is the first branchial muscle-plate, the lower end of which is detached from the pericardial wall. In the second branchial segment is the second branchial muscle-plate, the lower end of which is continuous with the pericardial wall. The difference between the two segments is owing to the slight retardation in development from before backwards—from segment to segment. I use the term ‘ muscle-plate ’ to denote those cells of the lateral plate which are obviously muscle-cells and the primordia of the branchial muscles. Though still containing yolk-granules they are distinguishable from the other cells of the lateral plate.

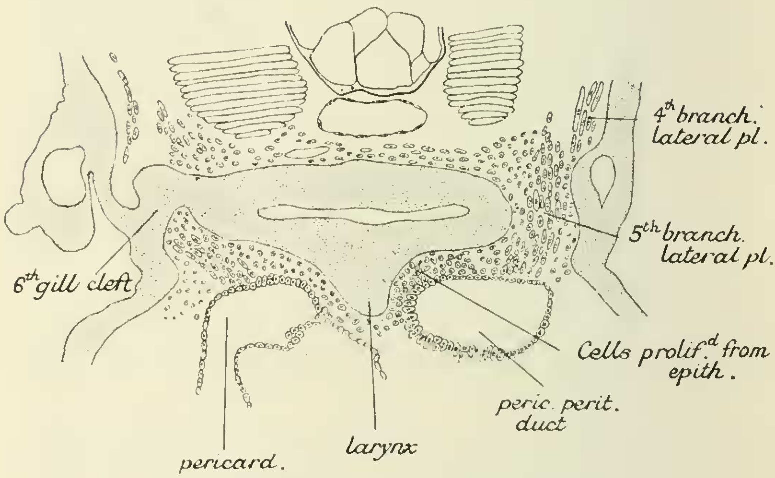
In explanation of the figures it should be added that in the 9·5 mm. embryos the branchial arches slope downwards and slightly backwards, in the 10·5 and 12 mm. embryos they are vertical, in the 16 mm. embryo they slope downwards and forwards.

I thus fail to find any continuity between the myotome above and the cell-columns in the first and second branchial segments in a 9·5 mm. embryo, i.e. at a stage when, according to Greil, such a continuity exists. The same is true of a 9 mm. embryo. Further, in a 10·5 mm. embryo what is obviously the second branchial muscle-plate is continuous with the pericardial wall. The difference in length of these embryos are so slight that it is improbable that—as is demanded by Greil's theory—what is ‘ lateral-plate ’ in the 9·5 mm. embryo is replaced by downgrowth from myotome in the 10·5 mm. embryo. Again, Greil's theory fails to explain why a muscle-plate derived from myotome downgrowth should ever be continuous with the pericardial wall. I also fail to find any differences in the shape of the cell-nuclei between the upper and lower parts of the cell-columns of these segments in the 9·5 mm. embryo, as is stated by Greil.

I am therefore of opinion that the evidences presented by these embryos are sufficient to warrant a rejection of Greil's statement that the branchial muscles are derived from downgrowths of the myotomes above, and to show that they are derived from the lateral plates—as is usual in Vertebrates.

What is said above in relation to the first and second branchial segments applies also to the third, fourth, and fifth.

Text-fig. 10.

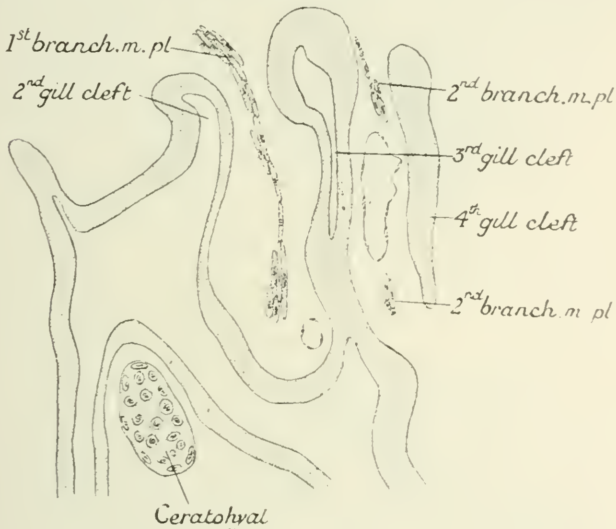


Embryo 11 mm., transverse section.

Constrictores branchiales and Levatores arcuum branchialium.—Both these muscles are developed in the first four branchial arches, but a Levator only in the fifth. Their anatomy in the adult stage was first described by Jaquet (1897), and subsequently—with more accuracy—by K. Fürbringer (1904). Greil stated that the Levators in the first four arches are developed from the upper part of the mesoblast (i.e. myotome downgrowth) in the arches, whilst the Constrictors are developed from cells given off from the muscles at their upper and lower ends. His words are 'welcher jedoch keinen Rest des primären den ganzen Bogen durchziehenden axialen Mesoderms bildet, sondern durch Züge spindeliger Zellen, welche von der Dorsal- und Ventralseite (Levatores und Interbranchiales) stammend, vorwachsen, geschlossen wird'. This occurs in the description of the 17·8 mm. stage (p. 1355). No figures were given illustrating this derivation of the Constrictors.

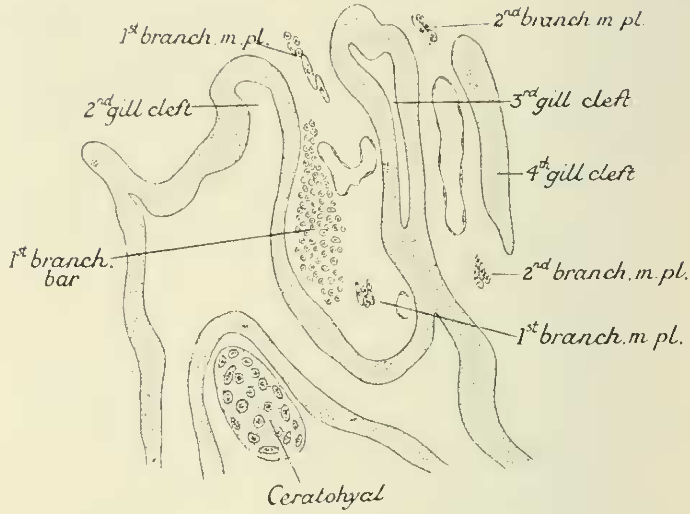
In 10·5 and 12 mm. embryos, and as is additionally shown in

TEXT-FIGS. 11–13.
Embryo 12 mm., sagittal sections; Text-fig. 11 is the most external.

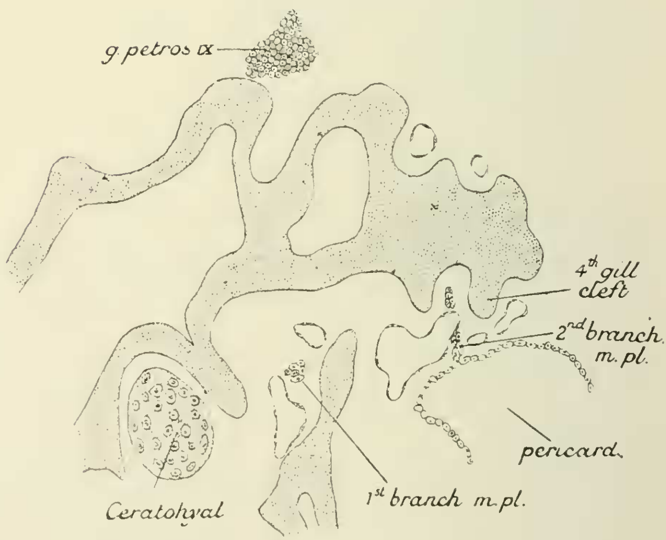


Text-figs. 11–13 taken from sagittal sections of a 12 mm. embryo, the first and second branchial muscle-plates form vertical strips through the whole extent of the arches. The ventral end of the first branchial muscle-plate is detached from the pericardial wall, and has grown a little forwards—towards, but not yet reaching, the Ceratohyal. The ventral end of the second branchial muscle-plate is continuous with the pericardial wall (Text-fig. 14). These muscle-plates, slightly convex outwards, pass down external to the primordia of the branchial bars.

TEXT-FIG. 12.

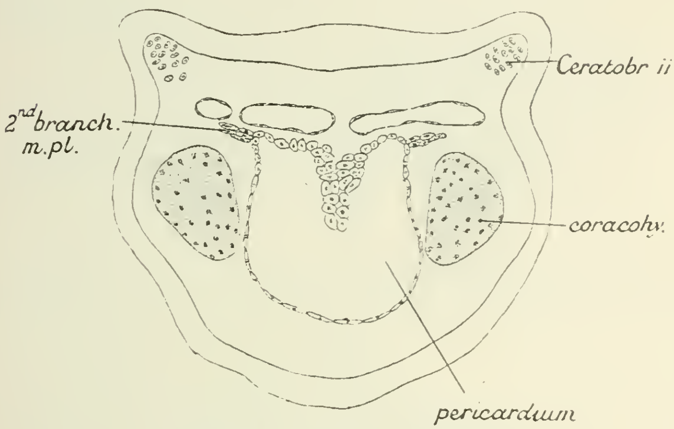


TEXT-FIG. 13.



In an embryo of 13·5 mm. (Text-fig. 15) the ventral end of the first branchial muscle-plate has separated and grown forwards to the Ceratohyal, forming the Branchio-hyoideus. The rest of the muscle-plate persists. The lower end of the second branchial muscle-plate has become detached from the pericardial wall and grown inward, forming the Transversus ventralis ii, and is detached from the vertical strip above.

TEXT-FIG. 14.



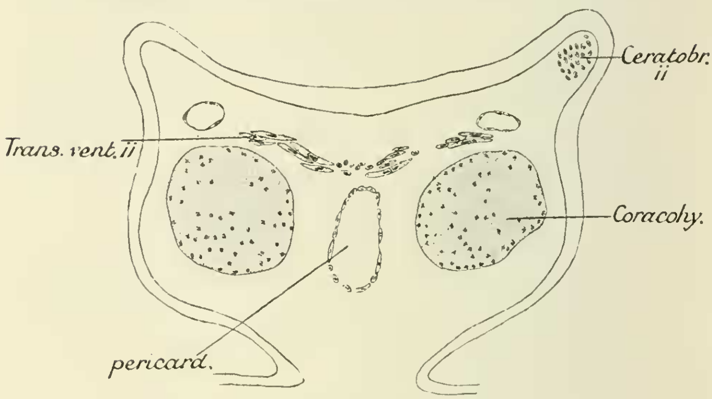
Embryo 12 mm., transverse section.

The development in the third and fourth arches is similar to that in the second.

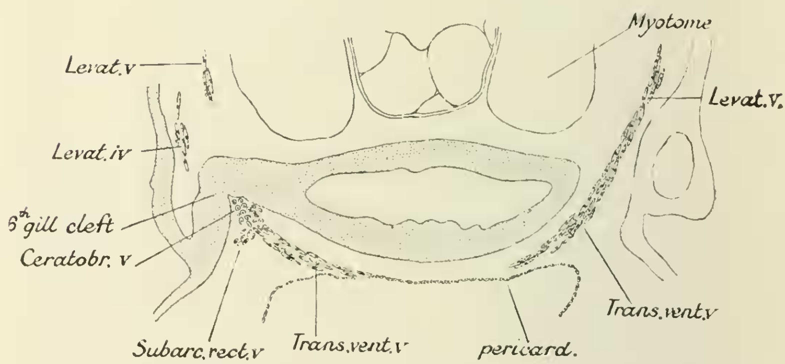
In an embryo of 16 mm. (Text-figs. 18–20) the first four branchial bars have separated into Epi- and Cerato-branchial elements and have chondrified, the process being most complete in the first. The upper end of the first branchial muscle-plate has separated into an inner and outer portion—the inner is the Levator and is inserted into the Epi- and Cerato-branchial i, the outer is the upper end of the Constrictor branchialis, which is continued down through the arch to its lower end. In the second branchial arch separation into these two constituents is not complete, and in the third and fourth branchial arches has barely begun, owing to the progressive retardation in development from before backwards. In a 17·5 mm. embryo the separation has occurred in these also. In a 27 mm. embryo the lower ends of the Constrictors have grown forwards. Each is attached to the lower end of the Ceratobranchial of the

Text-figs. 15–17.

Embryo 13·5 mm., transverse sections; Text-fig. 15 is the most anterior; Text-fig. 17 is 32μ behind Text-fig. 16.



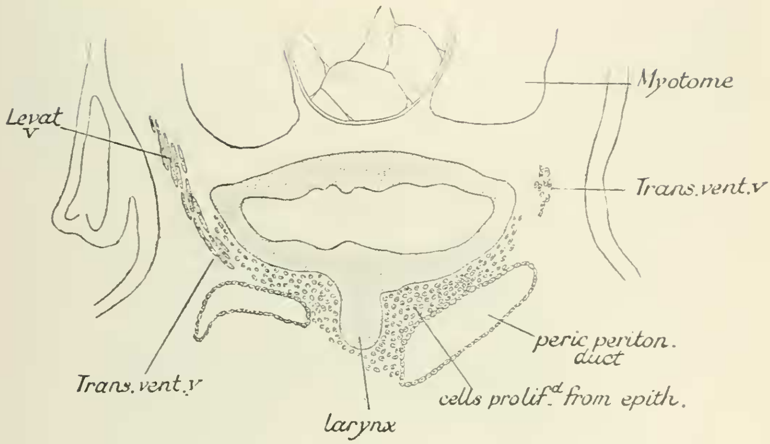
Text-fig. 16.



next anterior arch—the condition described in the adult by K. Fürbringer.

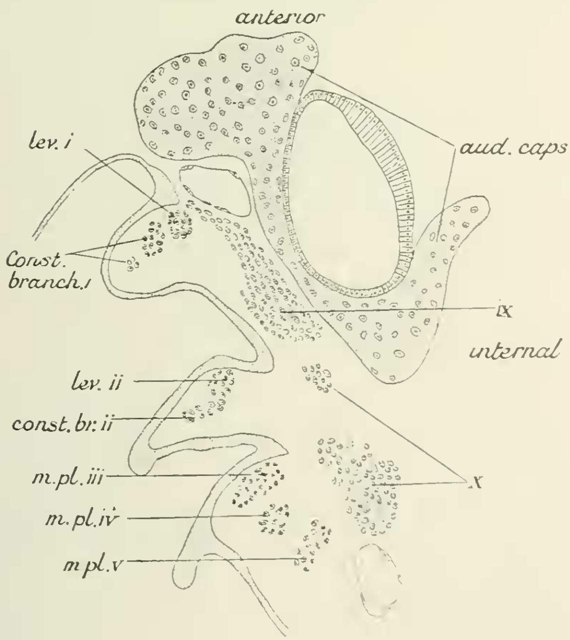
The above-recorded observations show that the Constrictores branchiales are the direct descendants of the branchial muscle-

TEXT-FIG. 17.



TEXT-FIGS. 18–20.

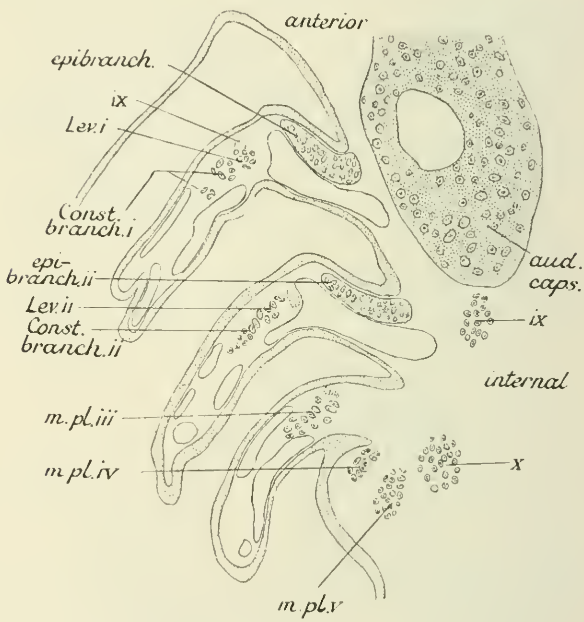
Embryo 16 mm., horizontal sections; Text-fig. 18 is the most dorsal.



plate, and that the Levatores arcuum are separated from their upper ends.

In the case of the fifth branchial arch Greil stated that the mesoblast (i. e. myotome downgrowth) forms the Dorso-pharyngeus. I find that the development is similar to, but not identical with, that of the more anterior arches. In the

TEXT-FIG. 19.

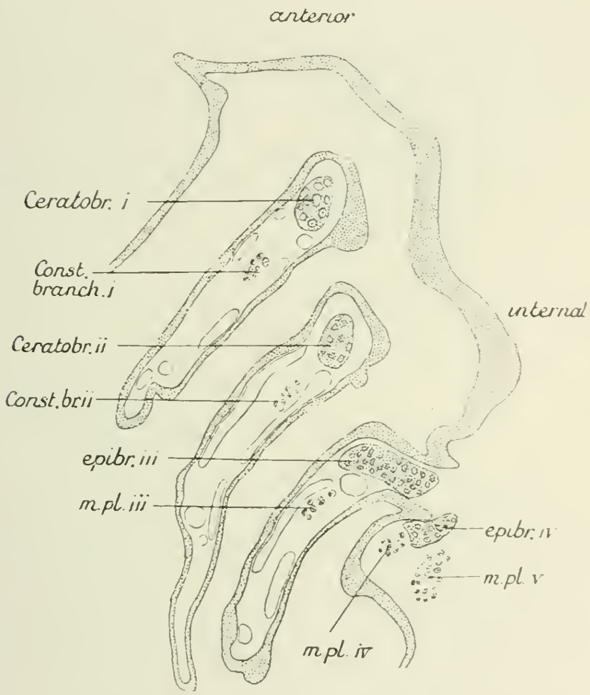


11 mm. embryo (Text-fig. 10) there is a lateral plate, the ventral end of which is continuous with the pericardial wall. In the 13·5 mm. embryo (Text-figs. 16, 17) the muscle-plate is formed; and its ventral end has separated from the pericardial wall and grown inwards forming the Transversus ventralis v. In the 16 mm. embryo some few fibres of the muscle-plate are attached to Ceratobranchial v., but the majority are continuous with the Transversus as in the 13·5 embryo. The condition is a more primitive one than in other arches. The upper part might be called a Levator or a Constrictor branchialis. The

Cucullaris is separated from it in a 14 mm. embryo—as was described by Greil.

It is not known whether the Constrictores branchiales and Levatores arcuum are present in Protopterus and Lepidosiren. Pinkus (1895) did not mention any individual branchial muscle

TEXT-FIG. 20.



in his description of the cranial nerves of Protopterus. The Constrictores are homologous with those of Selachii, the Levatores with those of Ganoids and Amphibia.

Subarcuales recti and Cleido-branchialis.—The Subarcualis rectus i. s. Branchio-hyoideus was first described by Fürbringer (1897), who stated that it is a muscle passing from the Ceratobranchial i. to the Ceratohyal. It was also described in the following year by Jaquet. Greil stated that it is developed from the ventral end of the mesoblast (i.e. myotome downgrowth) in the first branchial arch. As stated above, I find it to be developed from the ventral end of the first branchial muscle-plate.

Behind this muscle are two others, also longitudinal in direction—the Subarcualis rectus v. and the Cleido-branchialis. The latter was first described by Fürbringer under the name Coraco-branchiales, of which he said five are present, passing from the shoulder-girdle to the five Ceratobranchials. The fifth is the broadest and some of its fibres are attached to the skull. The others are slender. Greil described the development of these muscles as follows. The Subarcualis rectus v. is developed in a 17·8 mm. embryo by forward growth from the mesoblast (i.e. myotome downgrowth) of the fifth branchial arch. Its anterior end becomes attached to the ventral ends of the branchial bars. The Cleido-branchialis is derived from a process of the mesoblast of the fifth branchial arch which grows forwards, separating into three or four pointed extremities (' Zipfel ') which reach the ventral ends of the branchial bars. It forms an aberrant band of muscle which grows in the same direction, but is separate from the Subarcualis rectus v. and gains a secondary relation to the shoulder-girdle.

I find that these two muscles are developed from a single primordium which appears in a 13·5 mm. embryo (Text-fig. 16) as a slight forward growth from the junction of Levator v., and Transversus ventralis v. This primordium extends forwards, reaching the antero-posterior level of the third branchial arch in a 14 mm. embryo and that of the second branchial arch in a 16 mm. embryo (Text-fig. 28). In the last-mentioned stage its hinder part has increased in vertical depth and its postero-inferior angle is attached to the Cleithrum. In a 28 mm. embryo (Text-fig. 29) the primordium has fully separated into the muscles it forms, viz. the Subarcualis rectus v. passing from the fifth to the first Ceratobranchial, and the Cleido-branchialis. This latter muscle is posteriorly attached to the ventral surface of the Cleithrum and separates into fasciculi which, passing dorsal to the Subarcualis rectus v., are inserted into the ventral ends of all five Cerato-branchialia. The fasciculus inserted into the first is confluent with the anterior part of Subarcualis rectus v.

Innervation.—According to Fürbringer and Greil, Subarcualis rectus i. is innervated by the IXth. I can confirm this. According to Fürbringer the Cleido-branchialis is innervated by the Plexus cervicalis; according to Greil both the Subarcualis rectus v. and the Cleido-branchialis are innervated by the N. ultimus vagi (Quartus Vagi), i.e. the nerve to the fifth branchial arch. I can confirm Greil's statement.

The Subarcualis rectus i. s. Branchio-hyoideus is homologous with the similar muscle in Lepidosiren, Protopterus, and Amphibians. Its innervation is not known in these Dipnoans. In Amphibia, as in Ceratodus, it is innervated by the IXth.

The morphological nature of the hinder longitudinal muscles is uncertain. Fürbringer held that the Cleido-branchialis is homologous with the Coraco-branchiales of Selachii. Greil did not express any opinion other than that quoted above.

The muscles in Ceratodus are developed from a single primordium which grows forward from the fifth branchial arch. The posterior end of the muscle gains a secondary relation to the Cleithrum, and subsequently an almost complete separation into two muscles takes place. The shoulder-girdle is situated far forwards and has an oblique position—from dorso-posterior to ventro-anterior—its lower part underlying the branchial region. If this represents the phylogenetic development of the muscles, as is probable, the original form was probably a Subarcualis rectus v., passing from the fifth to the first Ceratobranchial, and the Cleido-branchialis is a secondary muscle. The developmental evidence thus leads to rejection of Fürbringer's theory.

It is not known whether there is a Subarcualis rectus v. in Protopterus and Lepidosiren, but Fürbringer described a homologue of the Cleido-branchialis in these Dipnoans and stated that the innervation is, as in Ceratodus, from the Plexus cervicalis.

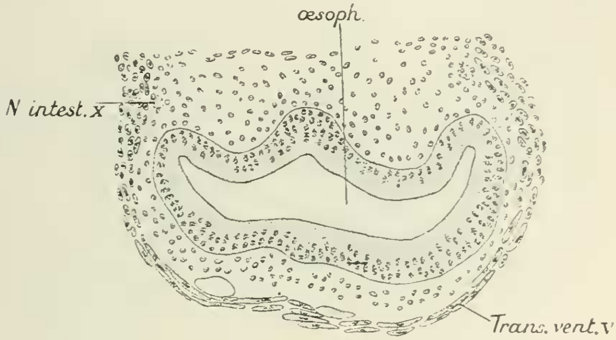
The Subarcualis rectus v. is probably derived from a Subarcualis rectus v. passing from the fifth to the fourth Ceratobranchial, and resembling the Subarcualis rectus iv a of Urodela in its forward extension to the first Ceratobranchial. I do not know of any homologue of the Cleido-branchialis in other groups.

Transversi ventrales ii, iii, iv, v are present—Greil stated that they are developed from the ventral ends of the mesoderm, i. e. myotome downgrowth, in the second, third, fourth, and fifth branchial arches by inward growth. I find that they are developed by inward growth from the ventral ends of the branchial muscle-plates (vide supra). I would add that Transversus ventralis iv. is not always developed, possibly owing to the relatively great size of Transversus ventralis v. Greil held that the Subarcualis rectus i. s. Branchio-hyoideus, developed in the first branchial arch, is serially homologous with the Transversi ventrales of the hinder arches. But it is difficult to think that a longitudinal muscle in one arch is serially homologous with a transverse one in another when neither changes its direction during development. In larvae of Ichthyophis and Siphonops a Subarcualis rectus i. and a Transversus ventralis i. are both developed in the first branchial arch. In Ceratodus, too, a Subarcualis rectus and a Transversus ventralis are developed in the fifth branchial arch. Transversi ventrales iv. and v. occur in Lepidosiren and Protopterus. The Subarcuales recti and Transversi ventrales are homologous or serially homologous with those of Ganoids and Amphibia.

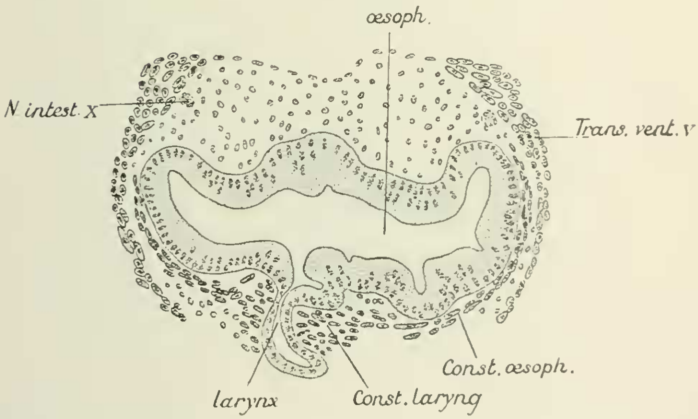
Transversus ventralis v. and Sphincter oesophagi et laryngis.—The Transversus ventralis v., as stated above, is developed in a 13·5 mm. embryo, as an inward growth from the ventral end of the fifth branchial muscle-plate (Text-figs. 16, 17). It extends back behind the posterior edge of the sixth gill-clefts to a greater degree laterally than in the median line, the distances being 96 μ and 40 μ, i. e. the posterior edge of the muscle is concave from side to side. The muscle in subsequent stages spreads backwards below the anterior part of the oesophagus (Text-figs. 21–4). This is concurrent with a backward shifting of the larynx (vide infra), so that in a 30 mm. embryo—the latest embryonic stage investigated—the larynx is not covered by the muscle.

TEXT-FIGS. 21–4.

Embryo 20 mm., transverse sections; Text-fig. 21 is the most anterior.



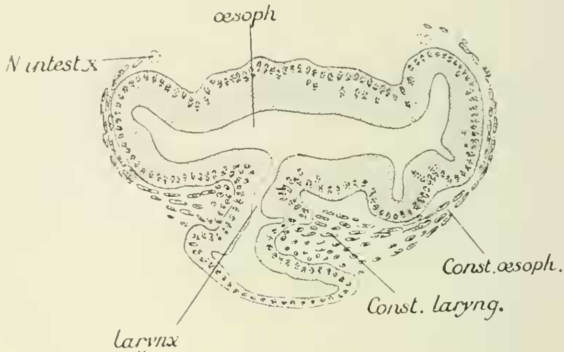
TEXT-FIG. 22.



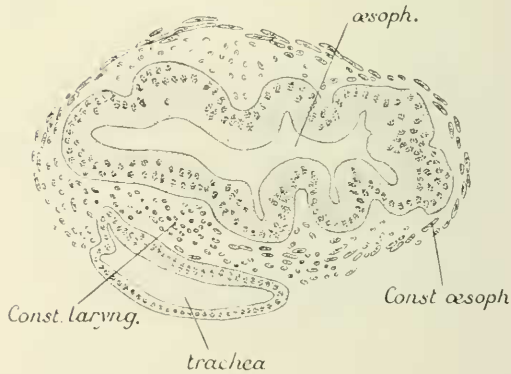
Greil represents the Transversus ventralis v. in his figure of a model of a 17·8 mm. embryo (Taf. lxiv, fig. 3) with a markedly convex posterior edge. But I have not found this in embryos of 14, 15, 16, 17·5, 20, 24, 28, and 30 mm. It is concave from the first and remains so during the extension backwards of the muscle, i.e. the posterior extension takes place as fast laterally as in the mid-line.

The posterior part of the Transversus ventralis v. forms the ventral constituent of the Sphincter oesophagi et laryngis, but

TEXT-FIG. 23.



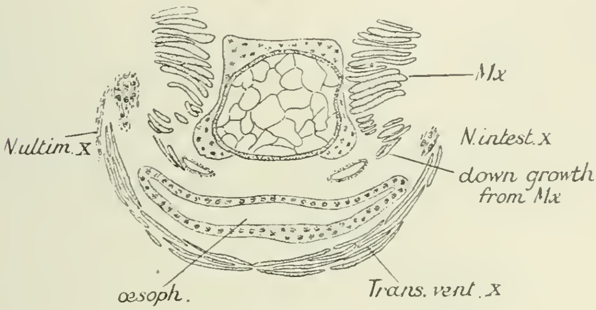
TEXT-FIG. 24.



no distinction can be made between the muscles. They form a continuous structure. The edges of the ventral constituent slightly lap round the lateral edges of the oesophagus in a 16 mm. embryo (Text-figs. 21, 22).

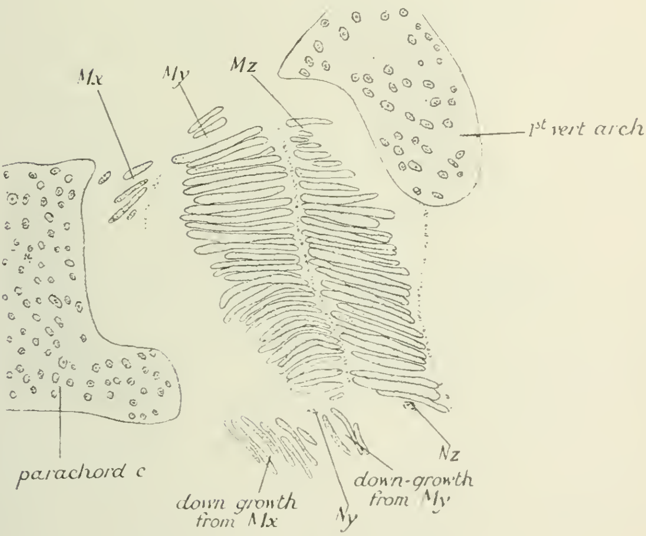
In a 24 mm. embryo (Text-fig. 25) a downgrowth takes place on each side from myotome x—downwards, backwards, and inwards, towards the upper part of the oesophagus, a little in front of the larynx. In one of 26 mm. (Text-fig. 26) this downgrowth has separated from its myotome, and there is a second

TEXT-FIG. 25.



Embryo 24 mm., transverse section.

TEXT-FIG. 26.

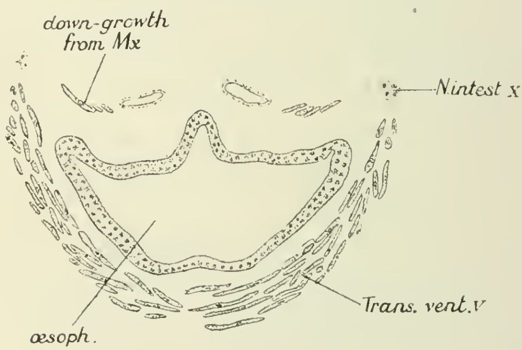


Embryo 26 mm., sagittal section.

downgrowth from myotome y. In an embryo of 28 mm. (Text-fig. 27) this, too, has separated from its myotome, and the two downgrowths form together a muscle-plate dorsal to the oesophagus. The Sphincter oesophagi et laryngis is thus developed from two constituents—a ventral derived from a backward extension of Transversus ventralis v. and a dorsal derived from the downgrowths of myotomes x and y.

The only changes which take place between this condition and the adult form (as determined by transverse sections) is that the Sphincter is completed by medial and lateral spread of its dorsal constituents, and it extends a little farther backwards in the mid-ventral line so as to underlie the larynx.

Text-fig. 27.



Embryo 28 mm., transverse section.

The Transversus ventralis v. is said by Greil to be innervated by the N. ultimus vagi, i.e. the nerve of the fifth branchial arch. My observations confirm this, and I can add that no additional branch of the vagus is developed in later stages for its hinder part, i.e. the ventral part of the Sphincter oesophagi et laryngis. This is in harmony with its development. The dorsal part of the Sphincter—developed from myotomes x and y—is innervated by branches of the Ni. occips. x and y, or by the latter only when there is no N. occip. x.

Wiedersheim (1904) described the adult condition of the Sphincter oesophagi et laryngis in all three Dipnoi,[1] and

[1] He gave figures of Protopterus and Lepidosiren, but not of Ceratodus.

Göppert (1904), subsequently, in Protopterus. These writers employed the term ' Constrictor pharyngis ' on the theory that it represents the musculature of atrophied hinder branchial segments. But the theory receives no support from the developmental phenomena in Lepidosiren, as described by Agar (1907), nor could I see any evidence in its favour in Ceratodus. I have therefore employed the term ' Sphincter oesophagi et laryngis '.

Agar stated that the ventral portion of the Sphincter oesophagi et laryngis of Lepidosiren is derived from cells budded off from the inner walls of the pericardio-peritoneal ducts, and its dorsal portions from downgrowths of the occipital myotome y (' possibly, but not probably, the downgrowth extends to x and z also '). These two constituents coalesce and form a complete sphincter muscle.

As, however, the ventral part of the Sphincter is continuous anteriorly with Transversus ventralis v. in all three adult Dipnoi, and this is not excluded by the figures given by Agar of the first stage of its development in Lepidosiren, it is possible that this part is, as in Ceradotus, due to a backward extension of Transversus ventralis v.

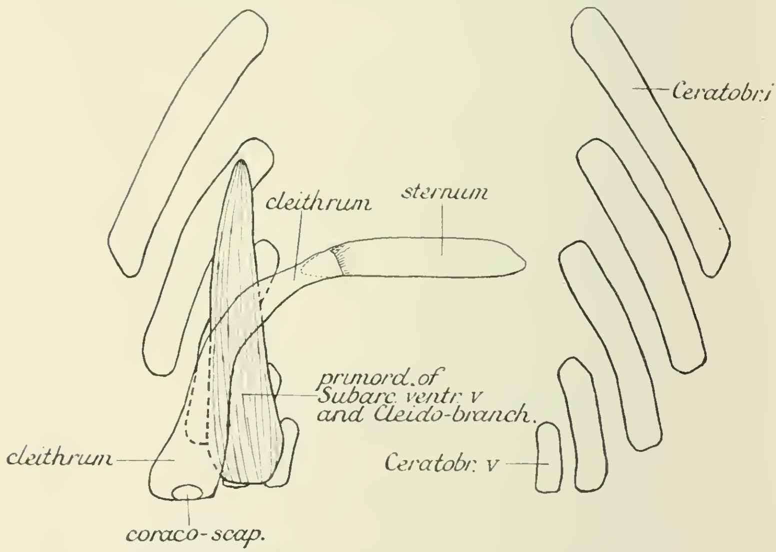
The ventral part of the sphincter of Lepidosiren is said by Agar to be innervated by the N. muscularis vagi. This is apparently the nerve of the fifth branchial arch, and the innervation would thus agree with that of Ceratodus. But the description given by Pinkus of the innervation of the muscles in the branchial region in Protopterus is very vague, and exact information is needed. The dorsal portion of the Sphincter of Lepidosiren is innervated, in accordance with its derivation, by Nervus occip. y (Agar): Lepidosiren and Ceratodus are similar in this respect.

L a r y n x.—Neumeyer (1904) stated that the larynx is developed in a 10·9 mm. embryo immediately behind the branchial region, Kellicott (1905) that it developed in a 11·6 mm. embryo in the ventral wall of the pharynx near the commencement of the oesophagus, Greil (1913) that it developed in a 11·6 mm. embryo at the level of the fifth branchial segment,

i. e. behind the sixth gill-clefts. No observer made mention of any subsequent backward shifting of the larynx.

I find that there is a slight trace of the laryngeal outgrowth in a 10·5 mm. embryo, but it is quite clear in a 11 mm. embryo (Text-fig. 10) as a median ventral outgrowth of the pharyngeal and oesophageal epithelium, extending from the anterior border of the fifth to 8 μ behind the posterior border of the sixth gill-cleft.

TEXT-FIG. 28.



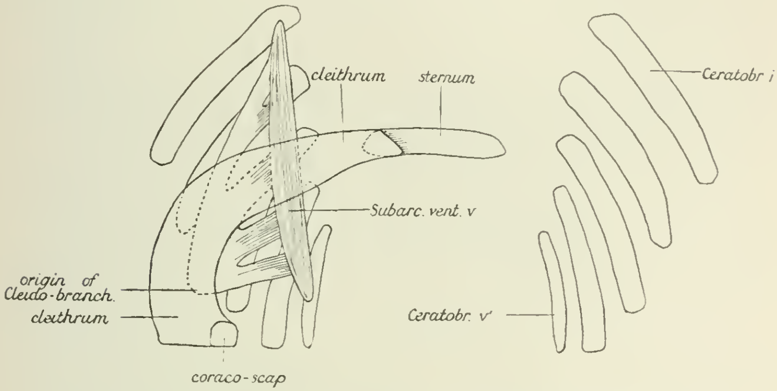
Embryo 16 mm. Model of Ceratobranchialia and Subarcualis rectus v.[1]

In a 12 mm. embryo the continuity of the laryngeal epithelium with the pharyngeal and oesophageal epithelium extends from 16 μ in front of the anterior border of the sixth gill-cleft to 72 μ behind it. In a 13·5 mm. embryo the continuity extends from 72 μ behind the sixth gill-cleft to 152 μ behind it. In a 20 mm. embryo it extends from 480 μ behind the sixth gill-cleft to 600 μ behind it, and the oesophagus opens into the stomach 140 μ

[1] In Text-figs. 28 and 29 only the front parts of the Cleithrum and Coraco-scapulare are represented. The epibranchialia i–iv are not shown.

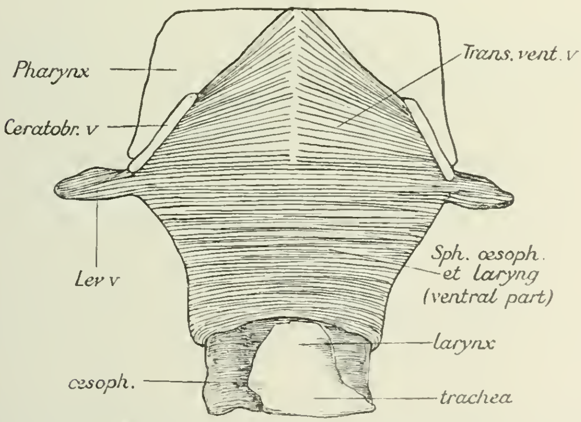
behind the posterior border of the larynx. The pre-laryngeal region of the oesophagus at this stage is thus 460 μ, the laryngeal region 120 μ, and the post-laryngeal region 140 μ in length. The above can be summed up in the statement that the larynx

TEXT-FIG. 29.



Embryo 27 mm. Model of Ceratobranchialia, Subarcualis rectus v, Cleido-branchialis, and shoulder-girdle.

TEXT-FIG. 30.



Embryo 20 mm. Model showing Transversus ventralis v. and Sphincter oesophagi et laryngis (ventral part); the laryngeal muscles are not represented.[1]

[1] Text-figs. 28, 29, and 30 were drawn by Miss Cross.

is developed as a median ventral outgrowth of the endoderm in the last (fifth) branchial segment and anterior end of the oesophagus, and subsequently shifts backward relative to the sixth gill-cleft so as to be situated entirely in the oesophageal region. During this period the larynx increases in size, though to a far less extent. Thus in the 12 mm. embryo the epithelium of the larynx is continuous with the endoderm above over a length of 86 μ from front and back ; in the 20 mm. embryo over a length of 120 μ. The trachea begins to be formed in the 13·5 mm. embryo as a posterior outgrowth of the larynx.

The larynx of Ceratodus is thus developed in the same position as in Menopoma, but unlike that of Menopoma it subsequently shifts backwards. The backward extension of Transversus ventralis v. is in relation to this. There is no similar extension of Transversus ventralis iv. in Menopoma.

Oesophageal and Laryngeal Muscles.—The only statement that Greil made in regard to these muscles is that in a 13·9 mm. embryo the free mesoderm cells increase in numbers round the oesophagus. These cells are chiefly of paraxial origin. They form a mantle round the gut and become for the most part smooth muscle-cells.

I find that a Constrictor oesophagi and a Constrictor laryngis are present in the adult, and that they are developed from cells which are budded off from the epithelium of the pericardio-peritoneal ducts in an 11 mm. embryo (Text-fig. 10). These cells increase in numbers and spread round the larynx and oesophagus, and in a 16 mm. embryo form the above-mentioned muscles, which are better developed in a 20 mm. embryo from which the figures are drawn (Text-figs. 22–4). The Constrictor oesophagi extends from the level of the anterior edge of the larynx to the posterior end of the oesophagus. In the laryngeal region its fibres are interrupted ventrally and pass towards the epithelium of the larynx through the fibres of the Constrictor laryngis. Behind the larynx the fibres encircle the oesophagus. The anterior part of the Constrictor oesophagi thus acts additionally as a dilatator of the larynx, but this part is continuous with the posterior part, and remains so up to the adult state. A separate Dilatator laryngis is not formed.

The Constrictor laryngis consists of short muscle-cells encircling the larynx in a horizontal plane. In transverse sections they are most obvious as such just in front and behind the larynx. The Constrictor laryngis gradually increases in size, and in the adult forms a muscle of many fasciculi which are penetrated by the dilatator fibres of the Constrictor oesophagi.

Innervation.—In a 27 mm. embryo the N. intestinalis x. passes back dorso-lateral to the oesophagus just within the upper edge of the ventral constituent of the Sphincter oesophagi et laryngis. At the anterior edge of the Constrictor oesophagi it gives off a ventral branch which passes to the larynx, the Constrictor oesophagi and Constrictor laryngis.

The oesophageal and laryngeal muscles of Ceratodus thus resemble those of Menopoma in that they are differentiated from cells which are proliferated from the splanchnic layer of the coelomic epithelium.

Pinkus described in Protopterus a fine twig from the N. intestinalis x. to the mucous membrane of the pharynx and larynx. This is the homologue of the laryngeal branch of the N. intestinalis x. in Ceratodus.

The evidence hitherto available suggests the probability that the Dilatator and Constrictor laryngis, and the Dilatator laryngis (and also the Constrictor oesophagi if microscopical examination shows it to be present) of Lepidosiren will be found to be developed from the cells which were shown by Agar to be proliferated from the pericardio-peritoneal ducts.

But, however this may be, comparison of the adult anatomy of Ceratodus, Protopterus, and Lepidosiren shows that the laryngeal muscles of Ceratodus—consisting as they do of a Constrictor laryngis and the (unseparated) fibres of the Constrictor oesophagi which act as a dilatator—are the most primitive existing in vertebrates.

I have the pleasure of thanking Dr. Bancroft for the embryonic and adult stages of Ceratodus, and the Bristol University Colston Society for defraying the expenses incurred in the investigation.

Relationship of Semon's Stages to Lengths of Embryo.

Stage 35	= 5·9 mm.	Stage 43	= 10·8 mm.
,, 36	= 6·4 ,,	,, 44	= 10·9 ,,
,, 37	= 6·6 ,,	,, 45	= 11·6 ,,
,, 38	= 8·3 ,,	,, $45\frac{1}{4}$	= 12·0 ,,
,, 39	= 9·0 ,,	,, 46	= 13·9 ,,
,, 40	= 9·8 ,,	,, 47	= 15·7 ,,
,, 41	= 10·2 ,,	,, 48	= 17·8 ,,
,, 42	= 10·3 ,,		

Synonyms.

Ceratodus.	
Genio-coracoideus.	Genio-coracoid, Humphry.
	Coraco-mandibularis, Jaquet, Greil.
	Coraco-mandibularis s. Coraco-cleido-mandibularis, Fürbringer.
	Unnamed, Maurer.
Coraco-hyoideus.	Coraco-hyoid, Humphry.
	Coraco-hyoideus, Jaquet.
	Coraco-hyoideus s. Coraco-cleido-hyoideus, Fürbringer.
	Cleido-hyoideus, Greil.
	Unnamed, Maurer.
Protopterus.	
Genio-thoracicus.	Genio-hyoideus, Owen.
	Deep layer of superficial stratum of ventral muscle, or Genio-hyoid, Humphry.
	Rectus inferior corporis (anterior part), Jaquet.
	Coraco-mandibularis s. thoracico-mandibularis, Fürbringer.
	Unnamed, Maurer.
Coraco-hyoideus.	Retractor ossis hyoidei + Coraco-hyoideus, Owen.
	Cervicalis profundus s. Coraco- or Ventro-hyoid, Humphry.
	Thoraco-hyoideus, Jaquet.
	Coraco-hyoideus s. Coraco-cleido-thoracico-hyoideus, Fürbringer.
	Coraco-hyoid, Agar.
	Unnamed, Maurer.

Lepidosiren.	
Genio-thoracicus.	Gerade untere Stammmuskel (anterior part of), Hyrtl.
	Unnamed, Maurer.
Coraco-hyoideus.	Retractor ossis hyoidei and Coraco-hyoideus, Hyrtl.
	Coraco-hyoid, Agar.
Ceratodus.	
Levatores arcuum branchialium.	Levatores arcuum branchialium, K. Fürbringer.
	Cranio-branchiales, Jaquet.
	Levatores arcuum branchialium (first four) and dorsal part of Dorso-pharyngeus (fifth), Greil.
Constrictores branchiales.	Branchiales, Jaquet.
	Interbranchiales, K. Fürbringer.
	Branchiales septales, Greil.
Cucullaris.	Scapulo-branchialis, Jaquet.
	Levator scapulae, Greil (1907).
	Dorso-clavicularis s. Trapezius s. Clavicularis, Greil (1913).
Subarcularis rectus i. s. Branchio-hyoideus.	Cerato-hyoideus internus, Fürbringer.
	Grand abducteur du premier arc branchial, Jaquet.
	Cerato-hyoideus, Greil.
Subarcualis rectus v.	Dorso-branchialis, Dorso-cerato-branchialis, Greil.
Coraco-branchialis.	Coraco-branchialis, Fürbringer, Jaquet.
	Coraco-branchialis, Cleido-branchialis, Coraco-cleido-branchialis, Greil.
Transversi ventrales ii and iii.	Muscle chiasmique, Jaquet.
Transversus ventralis ii.	Interbranchialis anterior, Greil.
Transversus ventralis iii.	Interbranchialis posterior, Greil.
Transversus ventralis iv.	Interbranchialis iv, Greil.
Transversus ventralis v.	Interbranchialis v. s. ventral part of Dorso-pharyngeus, Greil.
Sphincter oesophagi et laryngis.	Ceratodus. Constrictor pharyngis, Wiedersheim.
	Protopterus. Constrictor pharyngis et laryngis, Wiedersheim.
	Constrictor pharyngis, Göppert.
	Lepidosiren. Constrictor isthmi faucium, Hyrtl.

Sphincter oesophagi et laryngis.	Lepidosiren. Constrictor pharyngis et laryngis, Wiedersheim. Constrictor pharyngis, Agar.
Constrictor oesophagi.	Ceratodus, present.
	Protopterus, ?
	Lepidosiren, ?
Dilatator laryngis.	Ceratodus. Not a separate muscle.
	Protopterus. Dilatator, Wiedersheim. Pharyngo-laryngeus, Göppert.
	Lepidosiren. Dilatator, Wiedersheim.
Constrictor laryngis.	Ceratodus, present.
	Protopterus. Sphincter laryngeus, Göppert.
	Lepidosiren, ?

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NOTE.

On the development of the Quadrate and Epihyal.

The Hyomandibula of Ceratodus was first described by Huxley (1876), who stated that it is a small four-sided cartilage with a short conical process at its antero-ventral angle. This process is embedded in the dorsal and posterior part of the hyosuspensorial ligament.

The cartilage was subsequently described by v. Wijhe (1882), who identified it with a Hyomandibula, or possibly an Interhyal.

Ridewood (1894) stated that the hyosuspensorial ligament passes from the top of the Ceratohyal to a protuberance of

[1] The only copy of this in the United Kingdom that I know of is in the Library of the Royal College of Surgeons, Lincoln's Inn Fields.

the Quadrate. The Hyomandibula was always found dorsal to the ligament. It is a rhombic cartilage applied at its anterior edge to the 'cranial cartilage' (apparently the otic process), and with a ventral process which is attached to the upper surface of the suspensorial tubercle. The ventral process may be a separate cartilage. In one specimen he found a small accessory cartilage embedded in the ligament. Sewertzoff (1902) stated that the Quadrate is formed independently of the chrondrocranium and fuses with it by three processes —a 'palatobasal' uniting it with the trabecula, an 'ascending' uniting it with the alisphenoidal wall, an 'otic' uniting it with the external wall of the auditory capsule. He did not describe any pterygoid process. A Hyomandibula is present, lying just dorsal to the ligament connecting the top of the ceratohyal with the Quadrate.

K. Fürbringer (1904), in the 17·8 mm. stage, described a cartilage which lies behind the Quadrate, and, internally, is continuous with the anterior part of the auditory capsule. At an earlier stage the cartilage is separate from the cranium. This cartilage he identified as probably that described by Huxley. It did not exactly correspond in position with the Hyomandibula of Sewertzoff.

Krawetz (1911) stated that two cartilages are developed behind the Quadrate, one, the 'Hyomandibula' which lies in a cell-column ('Strang'), passing from the Quadrate to the auditory capsule, and a second, the Symplecticum, in close association with the ligament passing from the ceratohyal to the otic process of the Quadrate. These two cartilages are in connexion by a connective tissue, 'Strang'. The first-named of these cartilages is that represented by K. Fürbringer in his figures of the embryonic stage, the latter that represented by Sewertzoff. These two cartilages with the connecting ligament represent the upper part of the hyoid bar which is 'zerfallen' into two parts.

The statement of Krawetz that the upper part of the hyoid bar is 'zerfallen' into two parts appears to be an inference only, as he does not state that a single cartilage or structure had been seen in one stage and two cartilages in a succeeding one ; but the opinion he expressed is confirmed by the observations described below.

Greil (1913), who did not refer to the observations of Sewertzoff, K. Fürbringer, or Krawetz, stated that the Quadrate has a ' processus anterior (trabecularis) ' which springs from the trabecula and anterior portion of the parachordal, and a Processus oticus connecting it with the otic capsule. It has also (in a 11·5 mm. embryo) an inconstant, rudimentary, and transitory pterygoid process at the point where the Processus anterior springs from the trabecula.

In his figs. 421–3 (pp. 1154–6) he depicted a dorsal process of the Quadrate, naming it ' Proc. asc. Qu.' This, however, is evidently the otic process, which passes upwards and backwards to the otic capsule. On p. 1390 and in fig. 537, in his description of a 17·8 mm. embryo, he described and depicted a ' Knorpelspange ' which ' stellt eine secundäre Verbindung des Sphenolateralknorpels mit der Pars anterior des Palato• quadratus her '. This process is external to the N. ophthalmicus profundus (v.), and is evidently the ascending process of Sewertzoff.

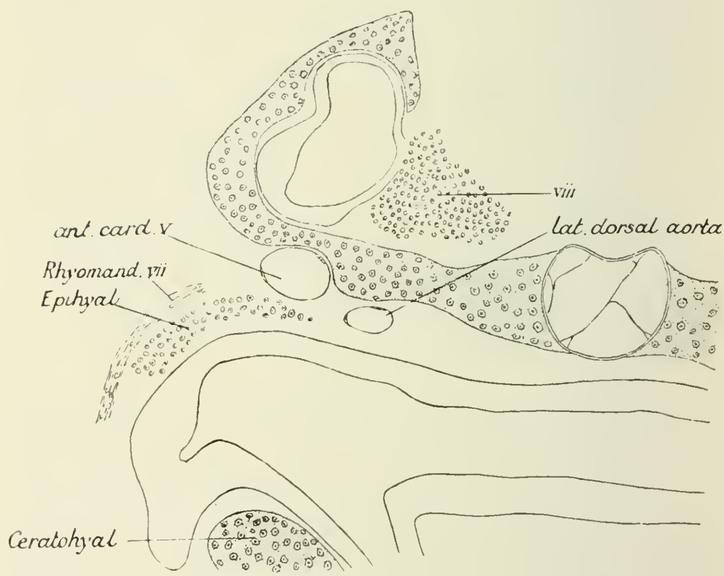
In a 17·8 mm. embryo, Greil described two or three egg-shaped or oblong pieces of cartilage adjoining the dorsal edge of the Ceratohyal and over which the N. hyomandibularis vii. (which passes out of the skull above the vena capitis lateralis and close under the otic process of the Quadrate) passes outwards. In the figs. 543 and 544 he depicted two small cartilages, the inner of which is ventro-external to the vena capitis lateralis. These cartilages he called Epihyalia s. Hyomandibularia. He also stated that a small cell-column passes from the dorsal corner of the ceratohyal to the lateral surface of the otic capsule and probably forms the primordium of small cartilaginous collections.

I find that the primordia of the Quadrate and Meckel's cartilage are first visible in a 10·5 mm. embryo as a continuous U-shaped column of cells on the inner side of the continuous primordium of the masticatory muscles and Intermandibularis.

It is not yet chondrified and not continuous with the trabecula or parachordal. In an 11 mm. embryo the primordium has separated into Quadrate and Meckel's cartilage, which are chondrified. The Quadrate is continuous with the junction of the trabecula and parachordal by a cartilaginous basal process, and also has ascending and otic processes which are continuous

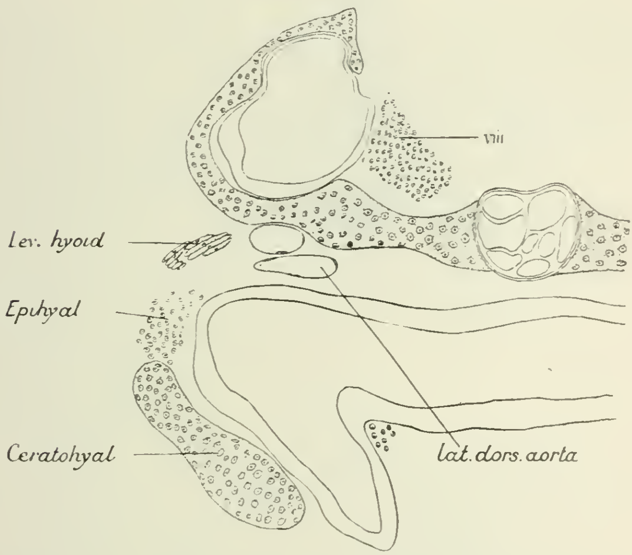
Text-figs. 31, 32.

Embryo 13 mm., transverse sections; Text-fig. 32 is 42μ behind Text-fig. 31.



with the trabecular wall and otic capsule. The upper ends of these processes are not chondrified until the 13 mm. stage. I have not seen any pterygoid process of the Quadrate in any one of several embryos of 11 and 12 mm. in length. The structures are depicted in Text-figs. 33 and 34 from a 13·5 mm. embryo. The observations thus confirm those of Sewertzoff. In a 13 mm. embryo (Text-figs. 31, 32) the Ceratohyal passes upwards and backwards in the hyoid segment. From the top of the Ceratohyal a curved tract of cells, the Epihyal, passes upwards and slightly forwards, and then inwards below the auditory capsule, but is not yet attached to this. The Epihyal has separated in a 13·5 mm. embryo into three parts (Text-figs. 35–7). The upper end—the primordium of the oto-quadrate cartilage—is slightly chondrified and connected by a narrow neck to the floor of the junction of the auditory

TEXT-FIG. 32.

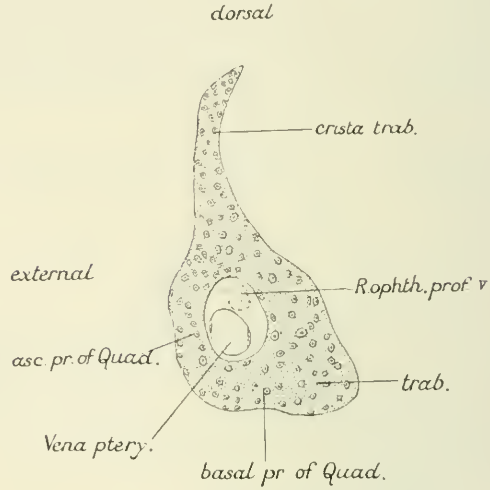


capsule with the parachordal. The middle portion—the Interhyal—is an aggregate of cells between the outer end of the oto-quadrate cartilage and the hyosuspensorial ligament. It is separated by a little gap from the former, but abuts against the latter. The lower end, consisting of cells in a slightly fibrillated matrix, is the primordium of the hyosuspensorial ligament. It does not yet extend forwards to the Quadrate, nor until the 17·5 mm. stage.

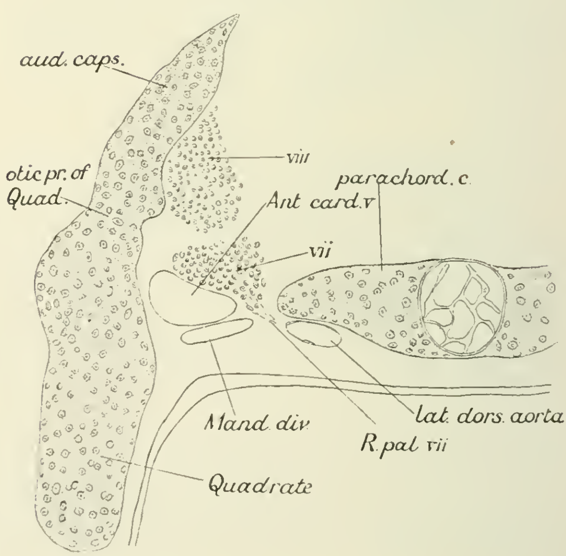
The outer end of the oto-quadrate cartilage joins the inner surface of the otic process of the Quadrate in a 17·5 mm. embryo. The Interhyal chondrifies in a 16·5 mm. embryo and subsequently enlarges (Text-fig. 38). In a 17·5 mm.

TEXT-FIGS. 33–7.

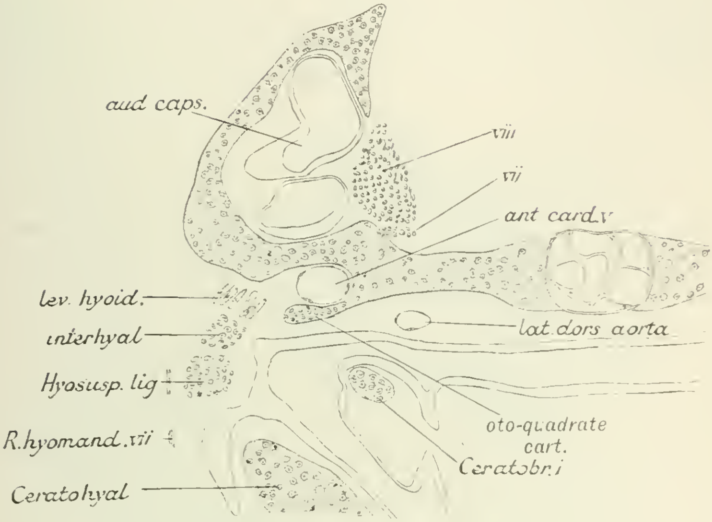
Embryo 13·5 mm., transverse sections; Text-fig. 33 is the most anterior.



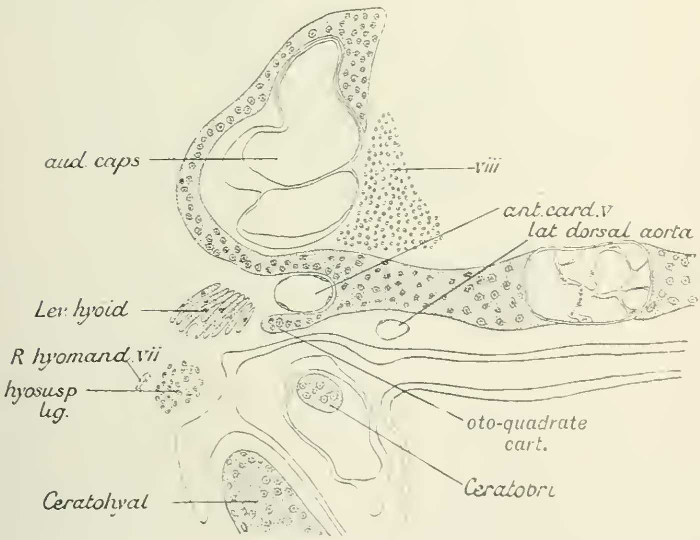
TEXT-FIG. 34.



TEXT-FIG. 35.

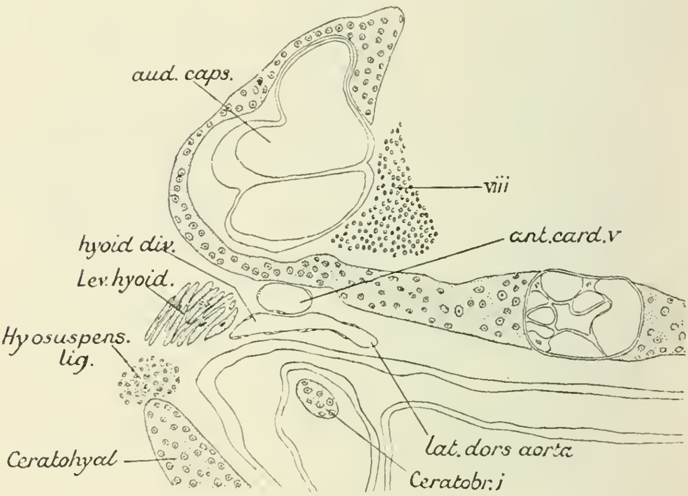


TEXT-FIG. 36.

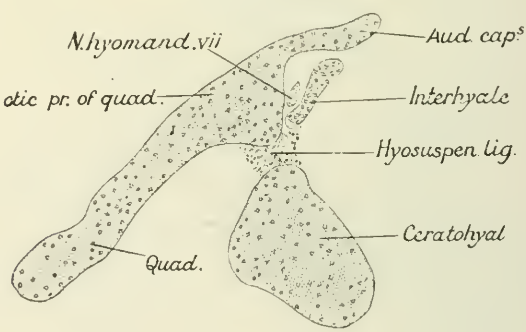


embryo the suspensorial tubercle has developed on the back of the otic process of the Quadrate and the anterior end of the hyosuspensorial ligament joins it. These structures are shown

Text-fig. 37.



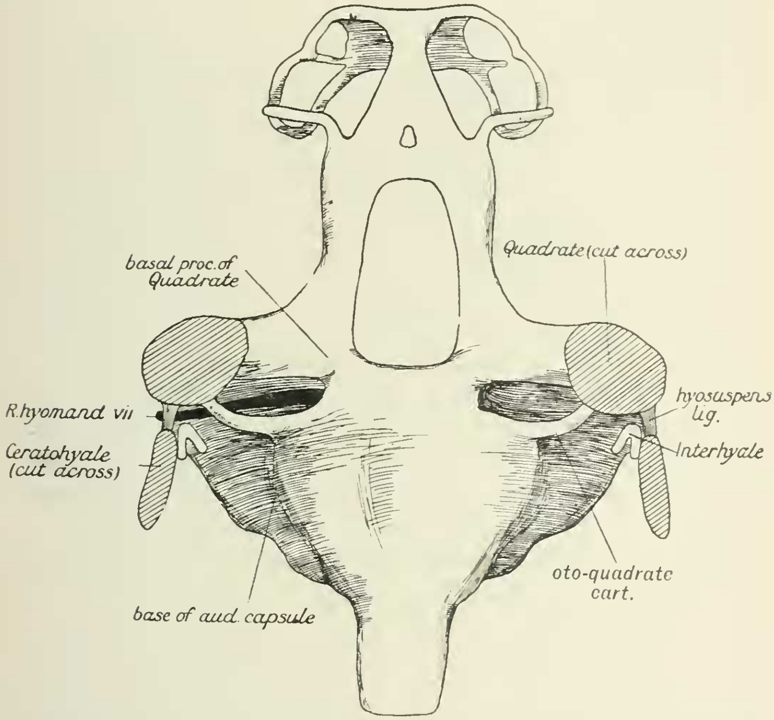
Text-fig. 38.



Embryo 26 mm., sagittal section.

in Text-fig. 39 made from a model of a 27 mm. embryo. The lateral end of the oto-quadrate cartilage turns forwards and joins the Quadrate. The Interhyal is a <-shaped structure, apex forwards, between the lateral edge of the auditory capsule and the hyosuspensorial ligament, and immediately behind the Quadrate. The ligament passes from the upper end of the Ceratohyal to the Quadrate. The R. hyomandibularis vii. passes outwards dorso-anterior to the oto-quadrate cartilage,

TEXT-FIG. 39.



Base of model chondrocranium of a 27 mm. embryo. The Quadrate and Ceratohyal have been cut across. The R. hyomandibularis vii. is represented only on the right side.

dorsal to its lateral end, then between the Interhyal and the Quadrate, and downwards external to the hyosuspensorial ligament.

The oto-quadrate cartilage is the structure called ' Hyomandibula ' by K. Fürbringer and Krawetz and probably the inner of the two ' Epihyalia ' depicted by Greil.

The Interhyal is the cartilage called 'Hyomandibula' by Huxley, Ridewood, v. Wijhe, and Sewertzoff, 'Symplecticum' by Krawetz, and the outer of the two 'Epihyalia' of Greil. The development, however, shows that no one of these names is quite suitable, and the second suggestion of v. Wijhe is adopted.

The hyosuspensorial ligament was so called by Huxley and succeeding authors.

Comparison of the upper end of the hyoid bar with that of the first four branchial bars suggests that the tract of cells which separates into the above-mentioned structures is serially homologous with the Epibranchialia, and it is accordingly called Epihal.

The above can be summarized as follows. A precartilaginous tract, the Epihyal, extends from the upper end of the Ceratohyal upwards and inwards beneath, though not at first attached to, the auditory capsule. This Epihyal separates into three portions—from above downwards the oto-quadrate cartilage, the Interhyal, and the hyosuspensorial ligament. The first-named gains secondary attachments. its inner end to the base of the chondrocranium and its outer end, subsequently, to the Quadrate. The Interhyal chondrifies later than the oto-quadrate cartilage. The hyosuspensorial ligament slowly extends forwards to the Quadrate.

Additional Literature.

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On Golgi's Internal Apparatus in spontaneously absorbing Tumour Cells.[1]

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With Plates 19 and 20.

Introductory.

The results obtained by the study of the Golgi apparatus of growing tumours of the mouse, rat, and guinea-pig were set forth in a previous paper (7) in which also the literature of the subject was summarized and discussed. The apparatus was found to be constantly present in the healthy cells of all tumours examined, in most of which it appeared with certain characteristic features. These were maintained through the successive regrafting of the same growths even when the general histological picture of some of them had somewhat changed and the tumour cells and their apparatus had become hypertrophic or had undergone partial degeneration.

It is now proposed to describe the behaviour of the apparatus during the spontaneous absorption of some of the same tumours, a point which could not be properly dealt with in the previous work. Such an investigation has not, as yet, been carried out, though it is important because it gives the opportunity for studying the modifications of the apparatus in cells of either epithelial or connective-tissue origin, undergoing regressive changes after a period of active proliferation, a phenomenon obtained with difficulty under different experimental conditions.

As shown in another paper (**6**), spontaneously absorbing

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